

## Bilateral Spores in New World Grammitid Ferns

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Most of the grammitid ferns, now placed by many authors in a separate family, Grammitidaceae, or a subfamily, Grammitidoideae, of the Polypodiaceae, were at one time classified as members of the genus *Polypodium*. In 1967 Morton wrote, "Evidence . . . has been accumulating in recent years that there are two major groups of species—those centering around the true *Polypodium*, as typified by *P. vulgare* L., and those belonging to *Grammitis* Swartz and some closely related small genera." Ching (1940) created a family, Grammitaceae, to accommodate these dwarf polypodies. In 1947 Holttum recognized the family, which he revised to Grammitidaceae, and later wrote (1955), "There are no intermediates between them and any true Polypodiaceae, and a close relationship seems very doubtful." After treating them, in 1947 and previously, as members of the Polypodiaceae, Copeland came to believe the group should have family status (1951). In her revision of *Grammitis* in New Guinea, Parris (1983) placed the genus in Grammitidaceae and gave a history of the family classification. Most authors have accorded the grammitid ferns family status, but W. Wagner (1973) retained them in a subfamily, the Grammitidoideae of the Polypodiaceae, and Tryon and Tryon (1982) placed them in a tribe, the Grammitideae of the Polypodiaceae.

The degree of relationship between the grammitid and the polypodioid ferns still remains, however, a matter of argument. Several presumably clear-cut characters separate the two groups. These have been discussed by de la Sota (1960) and Morton (1967). Evans (1969) gave a comparison of the Grammitidaceae with the *Polypodium pectinatum-plumula* complex, and Price (1983) contrasted *Polypodium*, *Pecluma*, and *Ctenopteris*, the first two in the Polypodiaceae s.s., the last in the Grammitidaceae.

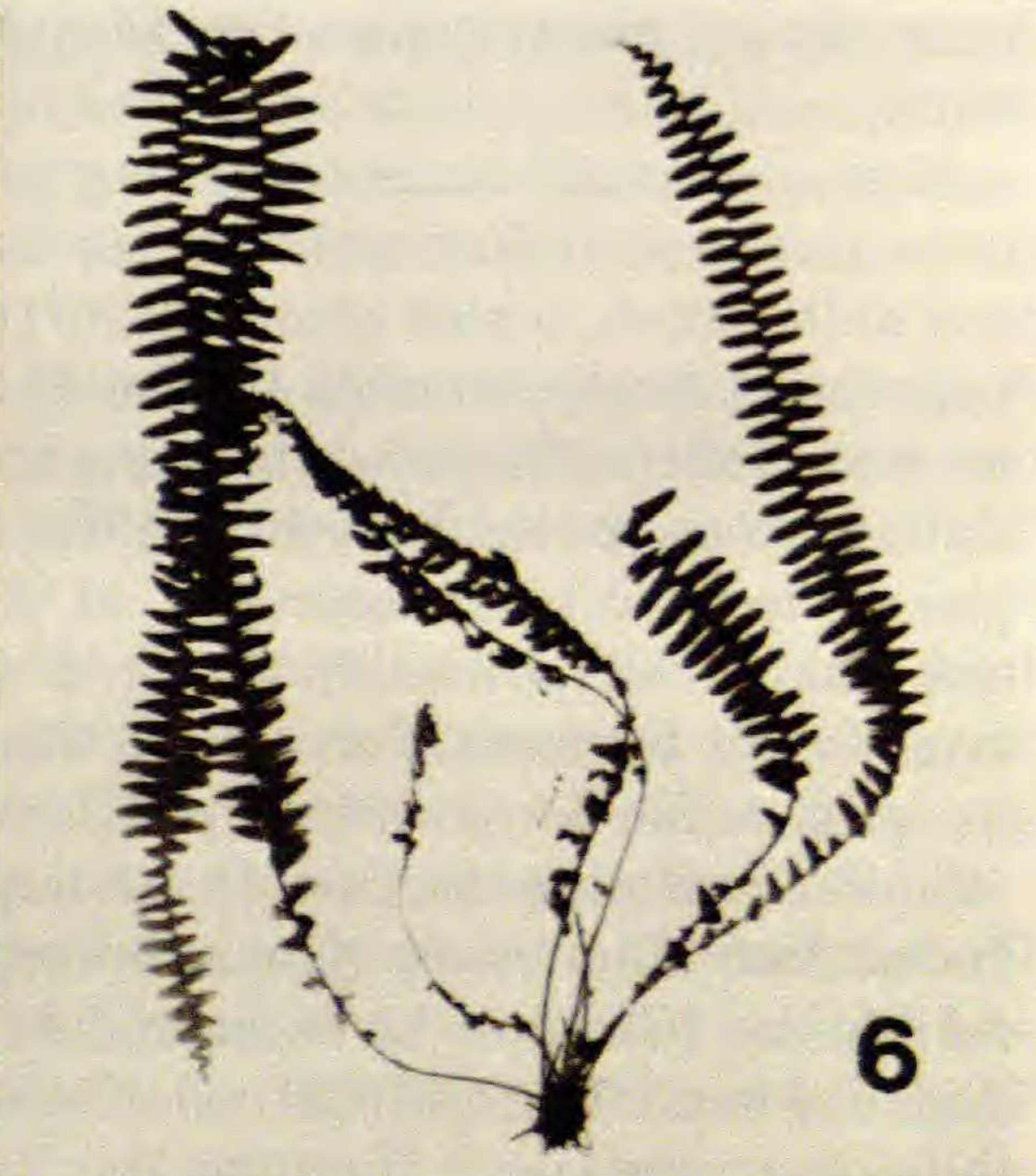
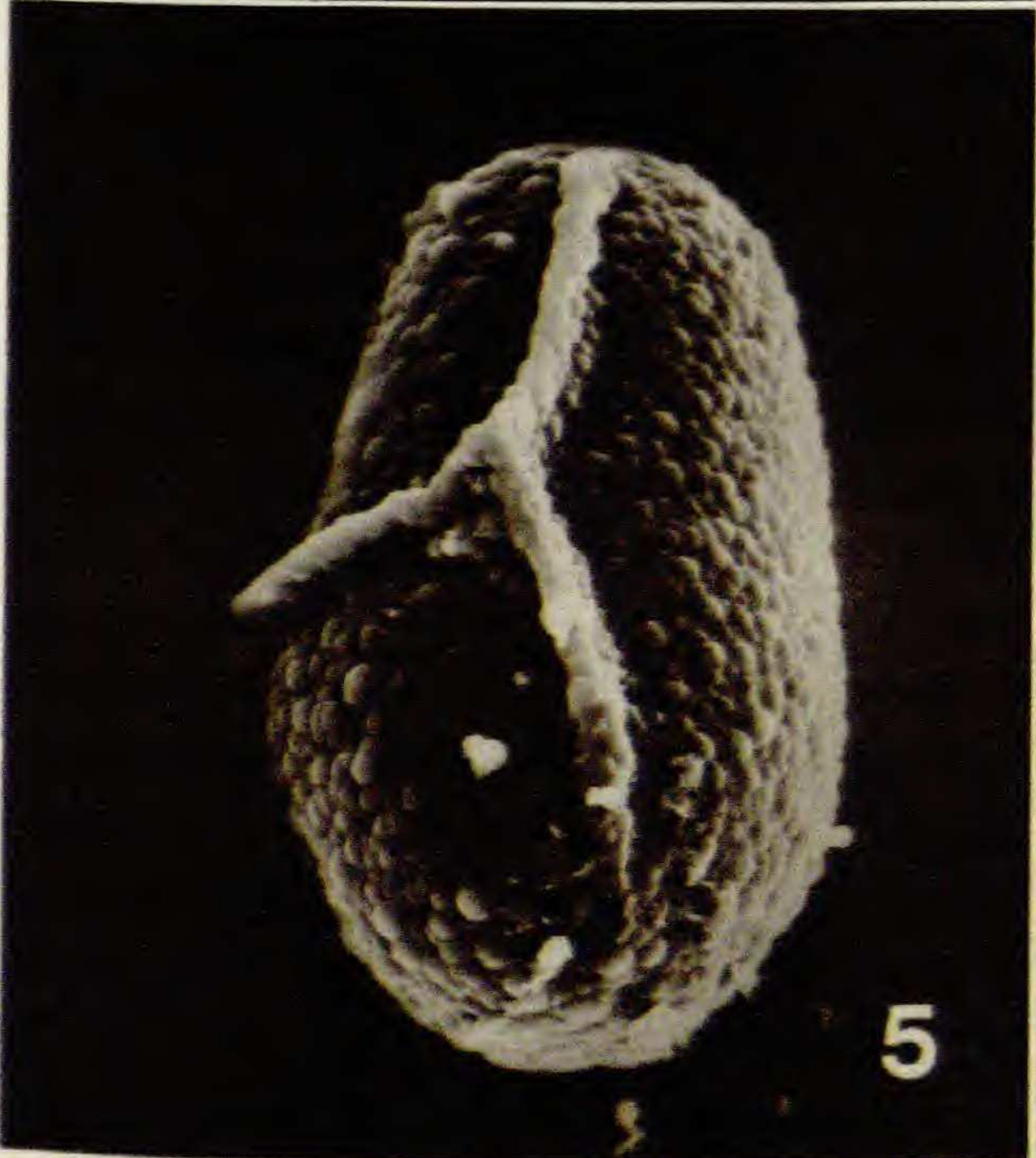
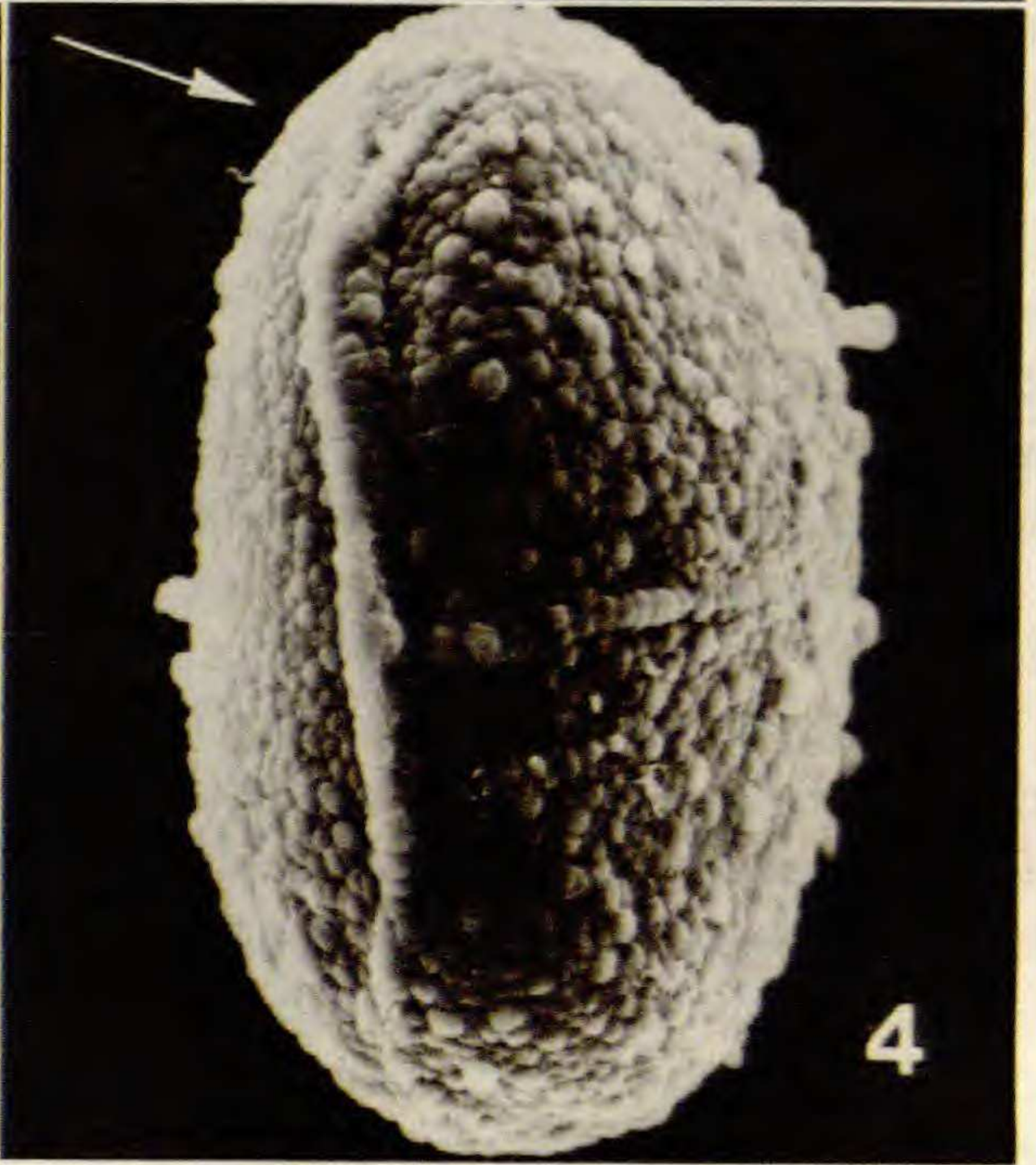
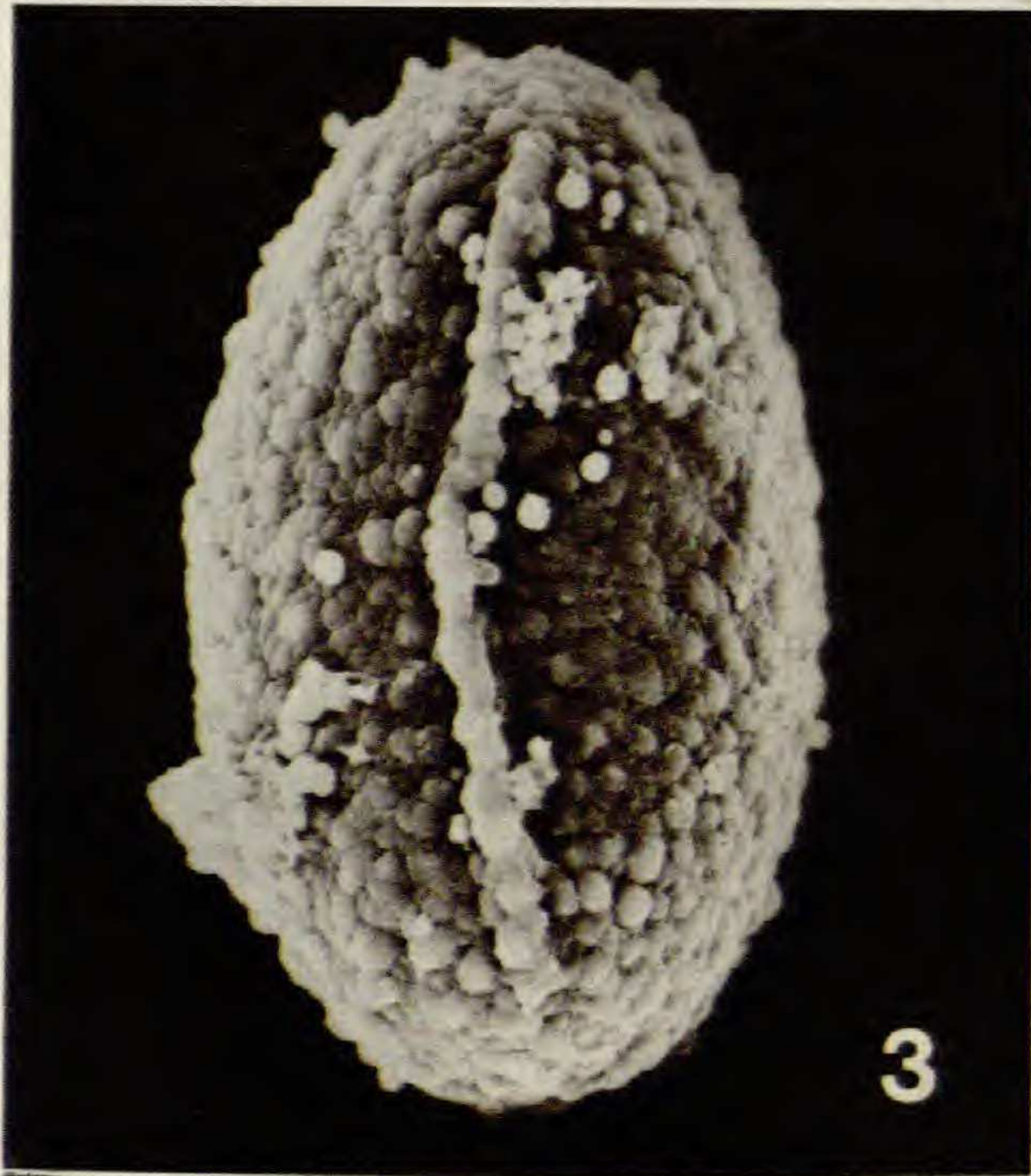
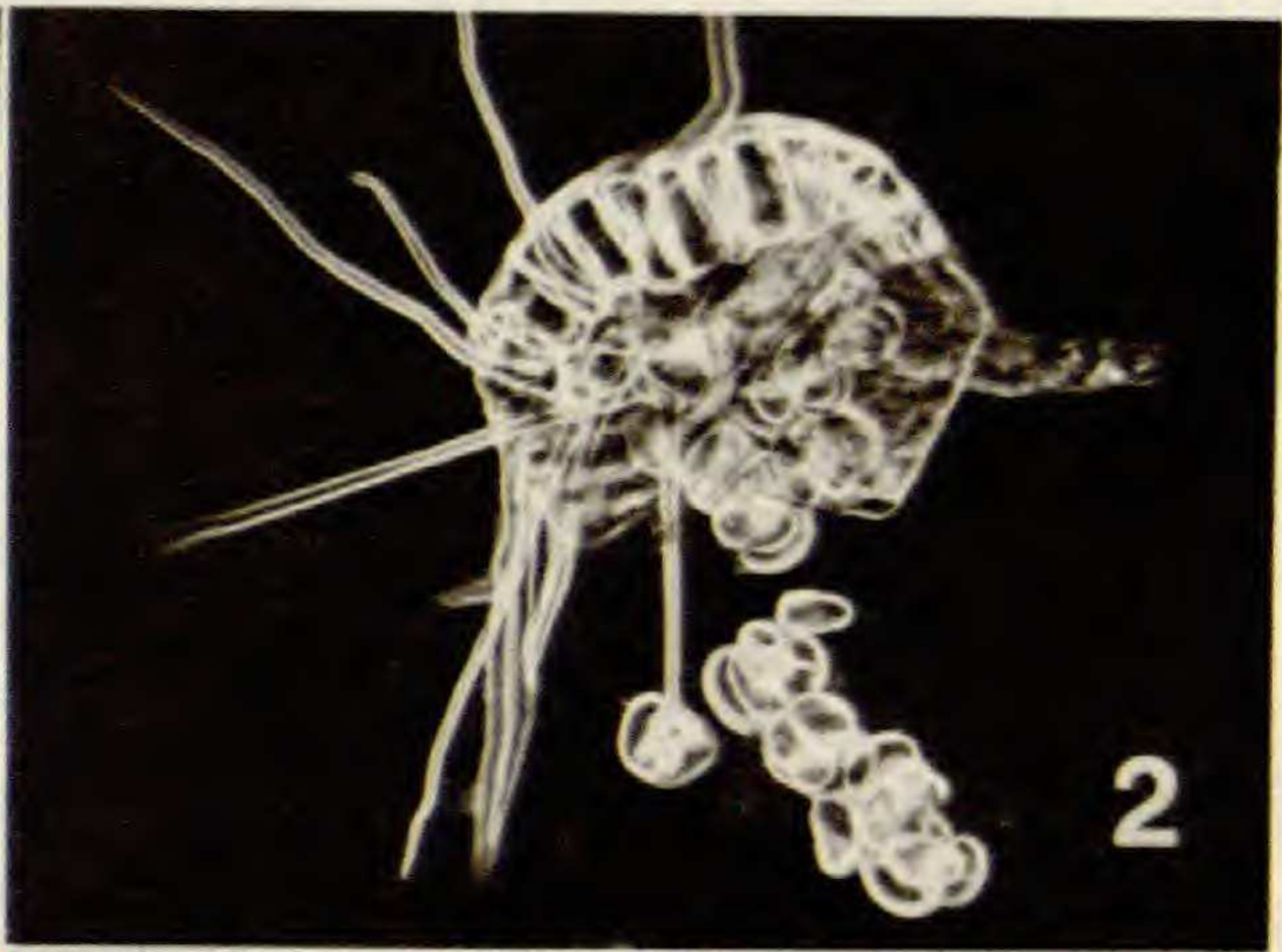
Briefly the distinctions between the polypodioid and the grammitid ferns are these: The Polypodiaceae s.s. have in general creeping rhizomes with scattered fronds, the grammitids have in general upright rhizomes and tufted fronds. Fronds of polypodies are often articulate, of grammitids, non-articulate. Scales of the former tend to be peltate and commonly borne on the leaf blades; those of the latter are basally attached and found only on the rhizome. The polypodioids bear scales and various types of hairs while the grammitid indument is typically composed of bristle-like setae often borne in pairs or multiples. Venation in the

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FIGS. 1-6. 1. Sporangium and spores of *Ctenopteris longa* (Buchtien 5252, MICH)  $\times$  80. 2. Sporangium and spores of *Grammitis lanigera* var. *lanigera* (Wagner 78528, MICH)  $\times$  80. 3-4. Scanning electron micrographs of spores of *G. lanigera* var. *lanigera* (Wagner 77062A, MICH)  $\times$  2500. Arrow in Figure 4 indicates fork in laesura. 5. Scanning electron micrograph of *G. lanigera* var. *stella* (Little 9356, US)  $\times$  2500. 6. *G. lanigera* var. *lanigera* (Wagner 77512, MICH)  $\times$   $\frac{1}{2}$ .







polypodioids is characteristically reticulate with free included veinlets; in grammitids the veins are usually free, or if reticulate, without included veinlets. The sporangial stalk in the polypodioids is composed of two or three rows of cells, in the grammitids only one. Spores of polypodioids are bilateral, monolete, and without chlorophyll; spores of grammitids are tetrahedral to globose, trilete, and have chlorophyll. Although exceptions may be cited to many of the above characters, spores have traditionally provided a dependable difference: "Possibly the most uniform and easily observable difference is in the spores, those of *Polypodium* being monolete and those of *Grammitis* trilete . . ." (Morton, 1967). Exceptions to this rule are the subjects of this paper.

Between 1977 and 1983 collections made in Costa Rica in connection with a cytological survey of the ferns of that country, included several specimens of *Grammitis lanigera* (Desv.) Morton var. *lanigera* [*Ctenopteris lanigera* (Desv.) Copel.]. In all characters this fern appears to be an incontrovertible member of the Grammitidoideae. However the correlation of characters is not perfect. The exception is the spores. These are conspicuously bilateral (Figs. 2-4). They are green with tuberculate surface and a single long laesura, which commonly has a characteristic bend or slight angle near the center (Fig. 3). In some spores the laesura forms an abbreviated fork (Fig. 4, arrow).

The sporangium bears setae and has a stalk composed of a single row of cells for most of its length (Fig. 2). The plants are tufted epiphytes with a short rhizome (Fig. 6). Spreading, stiff, one-celled hairs are borne on the stipe and blade, and the rhizome scales are basally attached and setose. *Grammitis lanigera* var. *lanigera* has been recorded from Costa Rica to Bolivia and has also been found in Martinique and Hispaniola (Morton, 1967). Our collections are from the following localities in Costa Rica (all are W. Wagner numbers deposited in MICH): Alajuela, Road N of San Ramón, 77062A; Cartago, Estrella, 79036; Tapantí, 83012; Heredia, Cerro Vueltas, 77008, 77013; Slopes of Volcán Barba above Porrosatí, 77512; Zurquí, 83019; Puntarenas, Monteverde, 83004B; San José, Cascajal, 78524, 78528.

Other grammitid ferns suggesting relationship to *Grammitis lanigera* were subsequently examined to determine their spore shape. One of these is *Ctenopteris stella* Copel., which Morton (1967) considered to be a variety of *G. lanigera*. A specimen from Colombia (Huila, 15 km SE of Garzon, Little 9356, US) and one from Bolivia (Cochabamba, King and Bishop 9677, MO) were found to have bilateral green spores, but with a different laesural pattern. In these the majority have a modified trilete scar (Fig. 5). Furthermore, the sporangial stalk differs from that of the type variety, and from nearly all grammitid ferns, in having two rows of cells for most of its length. Thus, Morton has combined as varieties in one species, two ferns with very different sporangial stalks.

Similar confusion has been found in plants named *Grammitis cultrata* (Willd.) Proctor from Guatemala (Quezaltenango, Aguas Jorgines, Skutch 904, MICH) and Mexico (Chiapas, La Independencia, Breedlove 33641, MICH; Volcán de Tacana, Matuda 2912, MICH) all of which have a single-rowed sporangial stalk, while other specimens from the last locality (Matuda S-225 and S-229, MICH) have two-rowed sporangial stalks. These differ also in the shape of the pinnae



which are shorter and more rounded in the last two collections. All of them have green bilateral spores and setose sporangia.

The same combination of characters, bilateral green spores and a two-rowed stalk together with a setose sporangium is found in two other grammitids, *Ctenopteris sericeolanata* (Hook.) Copel., which Morton thought to be synonymous with *Grammitis lanigera* var. *lanigera*, and *G. senilis* (Fée) Morton [*Ctenopteris senilis* (Fée) Copel.] from Central America, northern South America, and the Antilles, which Stolze (1981) placed in synonymy with *G. cultrata*.

Whether or not a single cell is to be found at the base of the two-rowed sporangial stalk in these ferns has not been determined. In *Prosaptia contigua* (Forster) Presl (Grammitidaceae) and in *Dictymia* J. Smith (Polypodiaceae) the sporangial stalk of two rows of cells is supported by a single cell. These are anomalies of uncertain significance in both families (Wilson, 1959). As a result of these observations, a broader consideration of polypodioid characters in grammitid ferns will be treated in a future paper.

Morton listed *Polypodium alternifolium* Hook. and *P. longum* C. Chr. [both are *Ctenopteris longa* (C. Chr.) Copel. according to Copeland, 1956] as two other species synonymous with *Grammitis lanigera* var. *lanigera*. A specimen of *P. alternifolium* (Ecuador, Sodiro, Aug. 1875, MICH), however was found to have tetrahedral spores. *Ctenopteris longa* (Bolivia, hacienda Simaco, camino a Tipuani, Buchtien 5252, MICH), on the other hand, has bilateral green spores like those found in our Costa Rican specimens (Fig. 1). Copeland (1956) in placing *P. longum* under *Ctenopteris* wrote: "Spores of South American specimens oblong; of Costa Rican, probably tetrahedral, but very few seen." He also described, as a new species, *Ctenopteris fabaespora* from Panama, basing the epithet on its bilateral spores. I have not seen a specimen, but according to David Lellinger (pers. comm.) Morton considered this fern to be the same as *Grammitis lanigera* var. *lanigera*. References, such as Copeland's, to bilateral spores in grammitid ferns are rare and have usually referred to the genus *Loxogramme*. Bilateral spores are known in *Loxogramme* in about half of the species, and although the genus has been thought by many to be a grammitid fern, evidence now seems to indicate that its relationships lie more closely with the polypodioid ferns (M. Price, pers. comm.).

Another suggestion that bilateral spores have been found in grammitids is that of Nayar and Devi (1965) who described the spores of *Ctenopteris brevivenosa* (v.A.v.R.) Holtt. as trilete-tetrahedral but added that many are monolete-bilateral. They also found *Prosaptia contigua* to have monolete-bilateral spores. Specimens of both these species (Singapore, Holttum 23319, MICH, and Sumatra, H. H. Bartlett 7963, MICH, respectively) were examined by me and neither was found to have bilateral spores. Thus there may be different spore types within the same species, or, perhaps, confusion about spore shape in certain Grammitidoideae may arise because of the widespread phenomenon of intrasporangial germination that occurs in this group of ferns (Stokey and Atkinson, 1958). At least three of the spores visible in my Figure 1 have divided. Sporangia are seen frequently with the entire contents at various stages of spore germination. Minute two-celled gametophytes, often with the spore wall still



TABLE 1. Selected Grammitid (G) and Polypodioid (P) Characters in Certain Grammitid Ferns.

	Spore			Sporangium	
	Color	Shape	Laesura	Capsule	Stalk
<i>Grammitis lanigera</i> var. <i>lanigera</i>	green <sup>G</sup>	bilateral <sup>P</sup>	monolet <sup>P</sup> with a bend	setose <sup>G</sup>	1 row <sup>G</sup> of cells
<i>Grammitis lanigera</i> var. <i>stella</i>	green <sup>G</sup>	bilateral <sup>P</sup>	modified <sup>?</sup> trilete	setose <sup>G</sup>	2 rows <sup>P</sup> of cells
<i>Ctenopteris longa</i>	green <sup>G</sup>	bilateral <sup>P</sup>	monolet <sup>P</sup> with a bend	setose <sup>G</sup>	1 row <sup>G</sup> of cells
<i>Ctenopteris sericeolanata</i>	green <sup>G</sup>	bilateral <sup>P</sup>	monolet <sup>P</sup>	setose <sup>G</sup>	2 rows <sup>P</sup> of cells
<i>Grammitis cultrata</i>	green <sup>G</sup>	bilateral <sup>P</sup>	monolet <sup>P</sup>	setose <sup>G</sup>	2 rows <sup>P</sup> of cells
<i>Grammitis</i> "cultrata"	green <sup>G</sup>	bilateral <sup>P</sup>	monolet <sup>P</sup> with a bend	setose <sup>G</sup>	1 row <sup>G</sup> of cells
<i>Grammitis senilis</i>	green <sup>G</sup>	bilateral <sup>P</sup>	monolet <sup>P</sup>	setose <sup>G</sup>	2 rows <sup>P</sup> of cells
<i>Polypodium alternifolium</i>	green <sup>G</sup>	tetrahedral <sup>G</sup> globose	trilete <sup>G</sup>	setose <sup>G</sup>	1 row <sup>G</sup> of cells

remaining, may appear oblong, when, in fact, they may have been formed from tetrahedral spores, and also swelling prior to division may make bilateral spores appear to be globose.

Variability in spore type and the occurrence of the two types of spores have been discussed by W. Wagner (1974). Within the same genus or very closely related genera, both bilateral and tetrahedral spores are known, for example, in *Gleichenia*, *Antrophyum*, *Vittaria*, and *Lindsaea*, as well as in *Loxogramme*. The situation in the grammitid ferns reported here is of special interest with regard to the relationships of the Grammitidaceae with the Polypodiaceae. All of the taxa discussed above have typical grammitid characters with important exceptions (Table 1). The occurrence of polypodioid characters suggests the possibility that the two groups of ferns may be more closely related than many authors have surmised. This study suggests, furthermore, that a re-evaluation of the taxonomy of this group of grammitid ferns is needed. Taxa that have been treated as synonymous or as varieties differ in characters that have usually been considered fundamental and conservative in the general taxonomy of ferns.

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## REVIEW

"*Ferns to know and grow*," by F. Gordon Foster. xiv + 228 pp. ISBN 0-917304-98-5. Portland, Oregon: Timber Press. 1984. \$29.95 (hardbound).

Third revised and somewhat enlarged edition of *The gardener's fern book*, reviewed in Amer. Fern J. 56:81, 1966. This edition is in a larger page format and additional species are treated. Unfortunately, the quality of reproduction of the photographs has suffered. It may be ordered from Timber Press, P.O. Box 1631, Beaverton, OR 97075.—A.R.S.